

CONSTRAINTS ON DEFINING THE 'LEVEL' AND 'UNIT' OF SELECTION

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ABSTRACT

A set of constraints forces trade-offs which prevent us from achieving the best possible definitions of the 'level' and 'unit' of natural selection. This set consists in decisions concerning conflicting pre-analytic intuitions in problematic cases, the relative roles of various conceptual resources in the definitions, which facts need to be accounted for using the definitions, how the relation between selection and evolution orients the definitions, and the relation between the level and unit concepts. Systematic reconstruction and evaluation of leading analyses along these dimensions favors a new functional analysis over Williams' consequentialist analysis, Sober's causal analysis, and Dawkins' teleological analysis.

Lumpers and Splitters. Review of the recent literature suggests that the units of selection debate in evolutionary biology has finally come of age. Two works are especially representative, i.e. Sober's (1984) book, *The Nature of Selection* and Brandon's and Burian's (1984) anthology, *Genes, Organisms, Populations*. Despite the sophistication of what has been achieved, I suspect that further progress will best be enhanced by reexamining the fundamental decisions which generated the analyses already given. In this paper I explore what is involved in two such decisions. Should we treat the units of selection concept and the levels of selection concept as equivalent; or should we differentiate them? On the basis of what sort of conceptual resources should we carry out our discrimination or lack of it, i.g., concepts appealing to effects, causes, functions, or ends?

Let me begin by citing some textual motivation for thinking about these questions. Brandon and Burian (1984) organize their anthology into three sections: historical readings, conceptual analyses, and models of selection. The second section is entitled "Levels and Units of Selection:

Conceptual Analyses". Why use both the term 'level' and the term 'unit', when either one suffices to focus the topic? They include an article by Brandon whose main point is that previous work has conflated two distinct issues, i.e., "What are levels of selection?" and "What are the units of selection?" The following point leaps out at readers of the anthology: the articles by Wimsatt, Lewontin, and Sober do not differentiate the levels and units concepts, whereas the articles by Brandon, Hull and Dawkins do so.

Do objects of some biological kind (e.g. genes, organisms, groups) form a unit of selection if and only if they form a level of selection? Sober (1984) presupposes an affirmative answer throughout his penetrating discussion of most of the major positions concerning the units debate. This presupposition has grave implications for Sober's full scale attempt to refute Dawkins' positions once and for all. Sober's string of related arguments against Dawkins' doctrine of the selfish gene are individually persuasive and collectively overpowering. That is, except for one point of detail so apparently insignificant one hardly notices it:

Dawkins (1978, 1982) has complicated his picture of the unit of selection problem, now seeing two quite different issues where *The Selfish Gene* saw only one. Instead of arguing that the gene is the unit of selection, Dawkins (1982, p. 82) distinguishes the issue of replicator selection from the issue of vehicle selection. (Sober, 1984, p. 253).

This is a misrepresentation. Dawkins' thesis of genic selectionism takes all selection, no matter at what level it operates (e.g. group versus individual), to be genic selection. He continues to hold that genetic replicators always form the unit of selection. Replicator selection concerns the units issue, whereas vehicle selection concerns the levels issue. The unit(s) issue concerns which objects ultimately benefit from selection pressures; on an evolutionary time scale, genes differentially benefit from selection pressures. The levels issue concerns which objects experience selection pressures; on an ecological time scale, organisms and possibly groups possess differentially adaptive traits (Holcomb, 1986--87). Dawkins could defend genic selectionism by claiming that Sober's points pertain to the level, not the unit. The price of Sober's failure to examine this contrast is that he has refuted genic selectionism only

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on the condition that the levels and the units concepts are equivalent. If the levels and units concepts are distinct, the adequacy of genic selectionism remains an open question. So the Sober-Dawkins debate turns on which supposition is true.

From this evaluation one would predict that those who discriminate the levels/units issues (unlike Sober) or who base their stand on conceptual resources other than causal notions (unlike Sober) should remain unpersuaded by Sober's battery of arguments. A point in case is Williams' (1986) commentary on Sober's (1984) book. Two ironies make us pause to wonder whether both parties "talk through each other", exhibiting partial lack of communication due to rival controlling presuppositions (remember Kuhn). The first irony concerns Sober's strategy for convincing his audience of his position in the levels debate. As Sober's student, I know that he regarded many criticism of his position as expressing misconceptions about the basic concepts of natural selection theory. So he devoted Part One of his book to clarifying concepts such as fitness, selection, adaptation; one cannot misunderstand such concepts and have much of a chance of resolving the levels issue. Hopefully, acceptance of his clarifications in Part One would lay the groundwork for acceptance of his stand on the levels issue in part Two.

The first irony is Williams' (1986, p. 122) modest comment that his disagreements are "mostly with limited passages in the second half of the book". Williams accepted Part One but not Part Two; and his disagreements are more fundamental than this quotation lets on (as we shall see). Another explanation is that Williams did not understand Sober's book or recognize how Part One supplies a basis for Part Two. These two interpretations need not be incompatible-opposing presuppositions render full understanding hard to come by. The second irony concerns this fundamental disagreement between Sober and Williams. It must have come as quite a shock to Sober that Williams (in Sober's eyes, 1986, p. 122) renounced the central insight of his classic book, the insight which Sober takes as his own point of departure.

In his comments on my book, Williams seems to draw back from what I think is the main conceptual insight in his book, *Adaptation and Natural Selection*. This is the distinction between group adaptation and fortuitous group benefit. He there gives the example of a

deer population in which individual selection for being fast (this being advantageous for evading predators) leads the average speed in the herd to increase. A consequence is that the population is less likely to go extinct. This is good for the group, but it is not a group adaptation, since group selection was not the cause.

The passage in which Williams allegedly rejects his own distinction reads:

I also find fault with Sober's concept of group properties and his stringent definition of group selection. Genes and, sometimes at least, gene pools have a stability of structure and continuity through time sufficient for such graphic modeling as mine above and Sober's (pp. 362-3). This means that groups with distinct gene pools are subject to natural selection on the basis of any properties that might give one group a greater likelihood of survival or proliferation than another. I agree with Sober that survival and proliferation must be biased rather than entirely random, but disagree that special kinds of bias are needed. He requires (pp. 261-2) that advantages and disadvantages in group-selection theory arise from group properties, some sort of multi-individual structure, rather than simply the properties of members. (Williams, 1986, p. 118).

Sober's interpretation is understandable. Suppose in this fleet deer case that benefit to the herd arises as a "statistical summation" of the effects of individual adaptations. In 1966 Williams (p. 17) told us that it was a mistake to infer that in such cases selection acts for the good of the group. In fact it acts for the good of individual deer and the group merely registers a beneficial effect from individual selection. Williams' definition of group selection in 1986 would have us treat this case as one of group selection; properties of the members of one group give it a greater likelihood of proliferation than properties of the members of another group. To this alleged definition Sober would reply that different causal processes correspond to different levels of selection; any definition of group selection which cannot distinguish two distinct causal processes at two levels from one causal process and its multi-level effects is inadequate.

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But Williams might maintain that the level of selection is to be identified in terms of heritable variation in fitness at that level, no matter how that variation is brought about, and that the statistical effect of individual fitnesses on group fitnesses is merely one process by which group selection operates. The group is the level even though the selection acts for the good of its members. Selection does not act for the good of the group in the sense of naive group selectionists who thought, for example, that altruism is promoted "for the good of the species". There is no fundamental change of position here—the population of deer herds evolves by group selection but there is no adaptation at the group level.

To adjudicate, Williams does maintain the distinction between group adaptation and fortuitous group benefit. Whereas Sober holds that an adaptation's being caused by group selection is necessary and sufficient for it to be a genuine group adaptation, Williams requires only that being caused by group selection is necessary for genuine group adaptation. So it is not decisive for Sober (1986, p. 122) to respond to Williams that a fortuitous group benefit "is not a group adaptation, since group selection was not the cause". That response depends on applying *modus tollens* to the conditional, "If trait A is a group adaptation, then group selection is the cause of A's prevalence". Williams agrees. Williams (1986, p. 119) holds that "I would find it confusing to use adaptive group properties as an axiom of group selection theory, rather than a measure of its importance". So what Williams denies is the conditional, "If group selection is the cause of trait A's prevalence, then A is group adaptation". In the fleet deer case, says Williams, A becomes prevalent by group selection, in that it helps the group avoid extinction from bear attacks, even though A is not a group adaptation.

What sort of approach allows cases in which benefits to groups arise as statistical summations if the effects of individual selection to count as a cases of group selection? Such an approach appeals to effects (even by statistical correlation) as the main conceptual resource for conceiving the level. Williams' appeal to correlated effects is just the sort of position which Sober is concerned to debunk. It is the reason why Sober's central conceptual contrast is between 'selection of' and 'selection for'. As evidence, consider how Sober (1984, p. 100) initially defines those terms:

"Selection of" pertains to the effects of a selection process, whereas "selection for" describes its causes. To say that there is selection for a given property means that having that property causes success in survival and reproduction. But to say that a given sort of object was selected is merely to say that the result of the selection process was to increase the representation of that kind of object.

Sober's contrast is obviously designed to handle the deer example. In the fleet deer example, Sober would have us say that there is selection for (properties of) individual deer and hence selection of individual deer, but there is no selection for (properties of) deer herds even though there is selection of the faster herd.

As a non-biological example, Sober (1984, pp. 99-100) describes a sorting toy, a toy which sorts balls by size. Balls drop through vertically arranged sieves as they fall, with each ball falling through sieves with holes larger than the ball and each ball settling on a sieve with holes just smaller than the ball itself. Suppose it so happens that the smallest balls are green and that the larger balls are some other color. In Sober's terms, there is selection of green balls. But why are green balls favored by selection? There is selection for being small, not for being green. The underlying rationale is that being small is the property which determines which balls descend the furthest and that being green is correlated with being small. 'Selection for' explains the pattern which 'selection of' merely records. In both the sorting toy and the fleet deer case there is selection of certain objects in virtue of a correlation within a causal situation. The increased disposition for success (falling to the bottom, enhanced fitness) found in green balls and in fleet herds is merely an effect due to a correlation to some causally efficacious property.

In sum, Sober's contrast between 'selection for' and 'selection of' marks a discrimination between causes and (correlated) effects, respectively. So we should find attribution of mislaid reliance on correlational rather than causal concepts as Sober's basis for rejecting inadequate stands on the levels issue. Consider Sober's charge that the mathematical analysis of variance in fitness is insufficient to identify the genuine level of selection in actual cases. Consider Sober's attack on the argument for genic selectionism which states that selection can always

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be represented in terms of the changing frequencies of alternative alleles. Both charges rest on the inability of statistically correlated effects to differentiate distinct causal situations. Sober's one (apparently) conclusive refutation of genic selectionism explicitly connects the notion 'selection of' to that of 'correlated effect'. Sober attributes an object having certain properties a probabilistic causal role just in case it increases the probability of the effect in at least one relevant context and lowers the probability in no relevant contexts. Do single genes always cause the effects selected for?

The problem is polygenic effects. If a gene raises the probability of a given phenotype in one context and lowers it in another, there is no such thing as the causal role that the gene has in general. Selection for or against the phenotype may cause the frequency of the gene to change, but this will be due to the correlation between gene and phenotype. There will be selection of the gene, but no selection for it. (Sober, 1984, p. 313).

This may not be the last word on genic selectionism. The phenomenon of polygenic effects has a counterpart at the phenotypic level. Like genes, a given phenotype appears to raise the probability of reproductive success in one context and to lower it in another, thereby having no causal role in general either. Sober has yet to show that no problem he finds in genic selectionism reemerges in modified form for selection at higher levels. However, my concern here is not with how best to explicate probabilistic causality, but with the prior step of choosing one kind of conceptual resource rather than another to elucidate the levels issue, e.g., effects, causes, ends. Even the dust jacket to Sober's book reminds us of Dawkins' basic position. Dawkins holds that vehicles (e.g. organisms, group, meta-groups) are built for the good of their replicators (the genes within them) but not conversely. Thus his basic contrast is teleological (see pp. 31-32 of this paper for a crucial caveat). Yet Sober never explicitly examines a teleological view of the levels debate. Hence, to the extent that Sober mistakes Dawkins' teleological position for a consequentialist position, Sober's whole way of attacking genic selectionism may well misfire.

Given the way Sober has reacted to Dawkins and the way Williams has reacted to Sober, we might forecast a stalemate in the levels debate.

te. To ward off more of the same, I propose to be deliberately crude and unsophisticated, trying to get "back to the basics". It is convenient to recast rival positions on the levels problem in a standardized, stylized format. The format offers a way to identify similarities and differences in various ways of handling the cases like that of fleet deer, fleet herds, and fleetness-coding genes. This format consists in reasoning focused on:

- (1) factual claims guided by pre-analytic intuitions about whether the level is the gene, organism, or group, or more than one;
- (2) a choice among various sorts of conceptual resources to define the level, e.g., consequentialist, causal, functional, or teleological;
- (3) definition of what we ought to mean when we call some kind of biological object a level of selection;
- (4) specification of what the concept so defined is supposed to account for;
- (5) methodological stance on the relation between selection and evolution;
- (6) determination of the relation between the levels and units of selection.

To evaluate the relative merits of underlying rival positions as recast in their stylized form, we shall appeal to a regulative ideal governing what we want our conceptual clarification to do for us. We want our analysis to help decide in problematic cases (such as the fleet deer case) whether selection occurs at one level or at more than one level of organization. We want it to define in a logically precise way (providing necessary and sufficient conditions) what in general a level or unit of selection is so as to illuminate the nature of selection. We want it to provide a definition which is secure in that it appeals to concepts as unproblematic as needed to account for what needs to be accounted for. Obviously, this ideal has already exerted force on the debate. I will turn out that no extant position does all these things equally well; there are trade-offs.

Let us take stock of where we have been and where we are going. I have proposed that the levels and units debate currently turns on

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two questions, namely (2) and (6). I have argued for this proposal by a review of recent exchanges and ironies between some of the main disputants in the debate. I shall now show how each of three types of analyses will handle points (1) through (4), namely the consequentialist, causal, and functional analyses. To facilitate comparative evaluation, I shall adopt the following method of exposition: for each type of analyses I shall cite its stand on (1)-(4) and explain, motivate or justify those claims, taken one at a time. The consequentialist analysis (1a, 2a, 3a, 4a,) reflects Williams' views. The causal analysis (1b, 2b, 3b, 4b) stylizes Sober's views. The functional analysis (1c, 2c, 3c, 4c) expresses my own views. I shall use the defects of the consequentialist and causal views to argue for the viability of a functional approach, an alternative heretofore hardly recognized and never developed. My own view is that the levels and units of selection concepts have distinct functional and causal contents. Then I will take up points (5) and (6), arguing for the superiority of functional analysis (5c, 6c) to both the causal (5b, 6b) and the teleological analyses. In so doing I hope to show that a functional approach is worthy of further examination.

Let me summarize the reasons for adopting a functional approach, reasons to be developed as we proceed. Functional analysis builds on what is right about the consequentialist and causal approaches; there is cumulative gain. Functional analysis is needed to make certain distinctions crucial for handling problematic cases, such as the fleet deer case; the other two approaches do not go far enough. If we need functional analysis then we should not regard 'function' as an inadmissible concept in selection theory just because that application is problematic. In fact, it is not so problematic as it first seems, provided we analyze it in terms of criteria for making a selection rather than purposes, goals, ends or other teleological concepts. Functional analysis justifies the claim that the units and levels of selection concepts are distinct, a view many hold without sufficient justification. Finally, functional analysis has the power to explain what other approaches assume, namely why fitness is identified the way it is, i.e., in terms of a propensity for reproductive success.

Consequentialist Versus Causal Analysis. Considerer consequentialist analysis.

(1a) Group selection occurs in addition to individual selection in

the example. Our intuition that group selection occurs derives from the positive correlation between fleetness and herd fitness. By "fitness" we mean the expectation or probability of success at survival or proliferation. The proportion of herds resist extinction and are composed of fleet deer exceeds the proportion of herds which resist extinction and are composed of slow deer. This consequentialist sense of group selection is not equivalent to naive group selectionism, the teleological view that in such cases selection "acts for the good of the group". Individual selection does not "act for the good of the individual", an equally teleological view. Teleological concepts are inadmissible for understanding selection theory in a literal sense; they are merely heuristic. We happily grant the causal analyst's point that the benefit to the herd arises as a statistical upshot of individual selection. However produced, the result is that groups are selected; there is selection of groups, even if fleet deer make fleet herds.

Although causal concepts (unlike teleological concepts) are admissible for understanding selection theory (fitnesses reflect the causal "power" of traits to produce reproductive success), such causal facts are irrelevant to fixing the level of selection. The effects determining selection at a level are non-random, but no special kind of bias in the effect is needed. Since the least problematic sense of non-randomness is correlation, we should not invoke problematic notions (e.g. causal or teleological concepts) which lead to unnecessary restrictions. Statistical effects of trait-environment relations on heritable variation in fitness differences generate a level.

(2a) There is selection of objects of some kind if and only if those objects exhibit heritable variation in fitness, where fitnesses are determined by character-dependent interaction of some (it does not matter which) objects with environment. 'Selection of objects' is a purely result-oriented concept with respect to the level of selection.

Causal analysis will no doubt object that although there is selection of groups there is no group selection because the herd benefits, not from its own traits, but from the traits of its members. But that objection rests on an unnecessary restriction inherent in models of Darwinian individual selection, namely that the same biological object possesses both fitness and the fitness-determining traits. Given the many ways models of selection deviate from Darwin's model, it is already too

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late to maintain that obsolete requirement. Thus Williams (1986, p. 118) is right to require for group selection only "that group with distinct gene pools are subject to natural selection on the basis of any properties that might give one group a greater likelihood of survival or proliferation than another". It does not matter which objects possess these properties; they may be individual or groups. This usage is traceable to the original Darwin-Wallace exchange about altruism: "selfish" traits promoted by individual selection benefit their possessor, whereas "altruistic" traits promoted by group selection benefit the group. In both cases the traits selected are possessed by individuals. The two levels of selection differ according to the results of selection.

(3a) Objects of some biological kind form a level of selection if and only if there is selection of those objects. That 'selection of objects' captures the sort of non-randomness found in a level of selection is further motivated by the nature of evolution by selection. As Lewontin (in Sober, 1984a) showed for each level in the hierarchy of biological kinds, the set of conditions necessary and sufficient for a population to objects to evolve by selection is that those objects exhibit character-dependent heritable variation in fitness. If the objects are herds, group selection occurs.

(4a) Any definition of a level of selection should explain why traits become prevalent or rare when selection occurs. The level of selection concept has intrinsic explanatory content. To explain why a trait changes in frequency when evolution by selection occurs, we establish the fitness benefits/costs of the trait. To be sure, doing so inevitably involves the notion that traits cause reproductive success—which shows that 'selection' is a causal concept, not that 'level of selection' is a causal concept. Thus, to understand why those herds members run swiftly have higher fitnesses than herds whose members run slowly, we need causal reasoning. But all the causal relations occur at the individual level; at the group level our explanation appeals merely to statistical results of those causal relations.

How well does correlational analysis fulfill our regulative ideal? It helps decide whether group selection occurs in problematic cases. The price is to devalue our competing intuition that group selection is only an appearance and not a reality. It offers a logically precise and general definition of selection at a level. The price is that it illumi-

nates the nature of evolution at a level by selection rather than selection at a level. In the fleet deer case group selection is only an appearance; it is not objectively distinct from individual selection. No consequentialist analysis has the resources to capture what makes levels of selection distinct. Committed consequentialists may hold that levels of selection cannot be objectively individuated. If so, they must provide a separate argument.

Because of the part-whole relation between objects in the biological hierarchy, traits and fitnesses at one level normally have consequences for traits and fitnesses at other levels. It is false that an adequate definition of a level of selection need not do more than to explain trait frequencies. On that definition in most actual cases of individual selection there will be selection at multiple levels. Suppose we were to accept that outcome. Then we must distinguish the sense in which individual selection is the basic level and the other levels are derivative levels of selection. To do so is to confront the original issue of what makes levels of selection objectively distinct. Two selection processes at different levels cannot be objectively distinct if the operation of one process results in the operation of the other process (say causal analysts) or if selection acts for the good of objects at one level and thereby for the other (say teleological analysts). Consequentialist analysis achieves high security by eschewing recourse to problematic concepts, but the price of failing to illuminate selection is too high a price to pay. So let us see what causal analysis has to offer.

(1b) Only individual selection occurs in the example. Our intuition here is that group adaptation and group selection are mirages produced by individual selection and individual adaptation. Thus Williams (1966, p. 17) notices that here we have a herd of adapted deer but no adapted herd of deer. Sober (1984, p. 208) defines adaptation so as to presuppose selection: A is an adaptation for task T in population P if and only if A became prevalent in P because there was selection for A, where the selective advantage of A was due to the fact that A helped perform task T. Sober departs from Williams by claiming in addition that A is a group adaptation for task T just in case it meets these conditions and the selective advantage of A was due to the fact that A is a group property which helped (in this case the group) perform task T. Selected for because it benefits organisms, fleetness also happens to benefit

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the herd (its benefit to the herd is a "fortuitous consequence"). Fleetness benefits the herd but it is not a group adaptation because it became prevalent by individual selection. Contrary to consequentialist analyses in terms of statistical variance, sober (1986, pp. 122-3) points out that the existence of group variance is not telling:

What is true of one herd holds for several. Suppose the herds are internally homogeneous for speed. The fast herds will be less likely to go extinct than the slow ones. But the reason is entirely due to the fact that there is individual selection on deer for being fast. It immediately follows that a sufficient condition for group selection is not supplied by the criterion that all the variance is between groups and none within. The question is not just how fitness varies, but why it does so. If an individual's fitness were determined by the average speed of the herd it inhabits, this would be group selection in my sense.

(2b) There is selection for property P if and only if objects vary with respect to whether they have P and those objects' having P causes selectively united objects to differentially survive or proliferate. This definition is at work in Sober's (1984, p. 280) causal definition of group selection. It employs both the concepts 'selection for properties' and 'selection of objects'. There is group selection for group that have some property P if and only if (a) groups vary with respect to whether they have P, and (b) there is some common causal influence on those groups that makes it the case that (c) being in a group that has P is a positive causal factor in the survival and reproduction of organisms. Clause (a) is needed because selection requires variants to select among. Cause (b) is needed to insure that the groups are part of the same selective situation. Cause (c) cites the difference crucial for objective distinctness. Suppose that being in a group of fleet deer is not a positive causal factor in the survival of individual deer. True, there is selection of groups, and selection of individuals, as defined in the consequentialist analysis. But whereas there is selection for individual properties, there is no selection for group properties. The definition clarifies why only individual selection occurs.

(3b) Objects of some biological kind form a level of selection if and only if there is selection for properties possessed by those objects

and there is selection of some objects. This is a mixed causal/consequentialist analysis, but the two kinds of concepts play different roles. The level should be identified in terms of which objects possess traits selected for (which pertains to causes) rather than in terms of selection of objects (which pertains to effects). Consequentialists try do too much with the concept 'selection of'. Conceiving the level by appeal to 'selection of objects' merely identifies the level by reference to the evolutionary results of selection. That's like defining acid via its effect of turning blue litmus paper red, rather than as proton-donor. In general, identifying definitions by reference to effects fail to illuminate the nature of the item identified; instead we should refer to its causal role to achieve that aim.

(4b) Any definition should explain not only why traits become prevalent or rare when selection acts but also why fitnesses vary. To explain why traits change relative frequencies it is sufficient, as consequentialists hold, to cite character-dependent heritable variation in fitness. But the level of selection concept has additional explanatory content, content absent from appeal to statistical correlations and effects. What is crucial is why fitnesses vary. To do so we need to refer to those objects whose traits cause success at survival or proliferation.

How well does causal analysis fulfill our regulative ideal? It helps decide whether in fact group selection occurs in problematic cases, but at the price of devaluing the competing intuition that there is a sense in which group selection occurs. It offers a logically precise definition designed to capture the nature of selection. But causal analysis is vulnerable to the charge that its price is a definition at the wrong level of generality. Consequentialist needn't be naive that they cannot discriminate correlations from causes or else confuse cause and effect, as causal analysts might have us believe. Arnold and Fristrup (in Brandon and Burian, 1984) acknowledge the causal nature of selection in general. Their point is that the causal nature of selection in general does not imply that the level of selection must be defined by reference to causes, i.e. "that the level at which we identify selection must also contain the causal network that determines the correlation between fitness and character value" (p. 298). Instead they use Price's statistical analysis of variance which distinguishes different selection processes in a levels

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hierarchy in accordance with the consequentialist definition previously given. That definition of a level of selection purposely leaves unspecified which level(s) enter into the causal interaction involving traits, environment, and success at survival and proliferation. Their reason for not individuating levels causally is that "Any attempt to qualify the concept of selection (at a level) by reference to the causal networks involved will result in the loss of a general definition of the process since there is no general causal chain" (p. 298).

That is, although for every level of selection there is a causal chain (which is guaranteed by the causal nature of selection), it is false that at a given level of selection there is always the same causal chain. Sober acknowledges this fact at the effect side of the causal relation (see his concept 'benchmark', 1984, p. 279). Group properties may make organisms benefit or suffer or else groups benefit or suffer. In each case group selection occurs. Sober reasons that which objects are affected by selection is irrelevant to fixing the level, as is evident from the fleet deer case. So the definition of group selection must be abstracted from reference to any particular level at the effect side of selection. That is, group selection occurs if and only if there is selection for group properties and selection of some objects, no matter at what level there is selection of objects.

But Sober has not acknowledged this fact at the causal side of selection. If not only group properties but also individual properties have univocal causal roles in a selection process, then it follows on Sober's account that the same selection process occurs at two levels! If the hierarchy consists in many interacting levels of kinds of objects, the possibilities for variation both in which levels register effects and in which levels bear causal properties are enormous. Any causal definition of the level will make assumptions about the causal network which unduly limit which models are genuine models of selection at a given level. Thus causal definitions will inevitably turn out to be too narrow or too broad.

Arnold and Fristrup distinguish between "a group-related effect on individual fitness" and "selection between groups as groups". Causal analysis counts as genuine group selection cases of selection between individuals on the basis of membership in a group and causal group properties. But such cases are merely cases of group-related effects

on individual fitness, not selection between as groups. This distinction is interesting, although the criterion for group selection 'selection between groups as groups' is as vague as it is obviously correct.

The basic problem, then, is to decide what sort of concepts we need to cash out the following general definition: selection at a given level occurs if and only if there is selection between objects at that level as objects at that level. For instance, group selection occurs if and only if there is selection between groups as such. Individual selection occurs just in case individuals are selected as such. In his effort to pry apart the concepts of selection and fitness (1984, p. 87), Sober's causal analysis has forsaken a pre-analytic intuition about how to unpack our general definition: (P) Selection at a level implies selection between objects at that level on the basis of fitness differences between objects at that level. In the case of group-related effects on individual fitnesses, there is selection between individuals on the basis of fitness differences between individuals but no selection between groups on the basis of fitness differences between groups. Since Sober's analysis counts such cases as paradigmatic of group selection, his causal analysis is doomed from the start (providing we retain (P)).

The preceding discussion leaves us with a quandary. Consequentialist analyses deliver definitions such that the level is given by which objects benefit or suffer, no matter who possesses the traits which cause these fitness benefits or costs. Causal analyses deliver definitions such that the level is given by which objects possess causally efficacious traits, no matter who receives fitness benefits or costs from those traits. Each side specifies what the other side claims must be left underdetermined. In order to adjudicate, we rely on pre-analytic intuition (P); if we were to give up (P) all other pre-analytic intuitions will become suspect and so we would give up an important resource for evaluating rival approaches. Consequentialist analysis satisfies (P) but fails to discriminate which sort of effects are used to identify the level. Causal analysis violates (P) and fails to discriminate which sorts of causes are used to identify the level.

The implication I draw is that we require an analysis which satisfies (P) and discriminates between types of causal roles and types of effects so as to pinpoint the way in which selection at a level is non--random with respect to that level. It was charged that consequentialist

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analysis failed to exhibit the objective distinctness of levels of selection. It was charged that the causal analysis failed to provide an appropriately general definition of level of selection. A crucial test will be to see whether the following functional analysis enables us to satisfy both the ideals of generality (in order to define the level in terms of necessary and sufficient conditions) and objectivity (so as to illuminate the nature of selection).

Functional Analysis. The following functional is designed to satisfy these desiderata.

(1c) Group selection occurs in one sense but not in another. Williams' talk of "fortuitous benefits" to the herd calls for a distinction between fortuitous and non-fortuitous effects. The sense in which individual selection occurs is that the benefit to an individual deer from its own fleetness is non-fortuitous. The sense in which group selection occurs is that the herd's benefit from its own high average fleetness is non-fortuitous. The sense in which individual selection is absent is that the individual deer does not benefit from the high average fleetness of its herd. The sense in which group selection is absent is that the herd's benefit from the fleetness of its members is fortuitous. Hence, the level should be conceived by reference to selection between objects on the basis of non-fortuitous or non-incidental effects to their fitnesses.

Sober's talk of "fortuitous benefits to the herd because of individual selection" calls for a distinction between effects which are part of a selection mechanism and effects not part of a selection mechanism. The benefit donated by individual fleetness to their possessors is part of a selection mechanism. The incidental benefit donated by individual fleetness to herds is not. Incidental effects accrue in virtue of a relation between objects/properties/fitnesses in the historical selective situation and one or more selection mechanisms operative in that situation.

This does not mean that individual selection by itself results in group selection, which would render the two levels of selection objectively inseparable. Rather, individual and group selection occur all along. The results of individual selection merely change the properties of groups which group selection acts on in virtue of the close relation between the individual trait 'fleetness' and the group trait 'average fleetness'. Two selection processes at different levels can be objectively distinct

even if the outputs of one process feed into the inputs of the other. The results of individual selection for fleetness change the average fleetness of the herd. Individual selection among individuals due to differences in individual fleetness is one level of selection. Group selection among groups due to differences in group average fleetness is an objectively distinct level.

(2c) There is selection for or against traits of objects of some kind if and only if there exist both fitness-donors and fitness-recipients in the same situation. Our central functional concept will be 'selection for sake of'. To distinguish it from 'selection for', we may generalize from the one-sided positive emphasis in 'selection for' to 'selection for or against'. Due to the relative character of fitness, whenever one form of a variable trait is positively selected another form is negatively selected. To achieve an analysis which discriminates between types of causes and types of effects on functional grounds, we shall define several types of roles corresponding to plausible candidates for being a level of selection. On Darwin's model, selection is a process "which helps those who help themselves". This common phrase embodies the idea that individuals have traits by which they donate fitness units to themselves. Talk of "donors" and "recipients" has proved invaluable in models of selection on altruism.

A "fitness-donor" is an object whose trait causally confers on some object some component of the second object's fitness. A "fitness--recipient" is an object whose fitness has a component causally conferred on it by some object's trait (in virtue of the trait's effect on the first object's fitness). These two concepts are complementary with respect to the trait selected for or against. By "causally confer" it is not implied that fitnesses are causes or effects, but only that fitnesses are assigned on the basis of cause-effect relations (see Sober, 1984, chap. 3). Two derivative notions are now definable. A "fitness-effector" is an object participating in the determination of fitness of some object because the trait of the fitness-donor is relational or is influenced by relations to other objects. A "fitness-effectee" is an object whose fitness is changed as a result of the change in fitness of some fitness-recipient due to some trait selected for or against. These terms clarify our intuitions about the original example. With respect to the individual trait 'fleetness' individual deer are fitness-donors and fitness-recipients, nothing

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is a fitness-effector, and the herd is a fitness-effectee. With respect to the group trait 'average fleetness' herds are fitness-donors and fitness-recipients, individual deer are fitness-effectors, and nothing is a fitness-effectee.

(3c) Objects of some biological kind form a level of selection if and only if those objects are fitness-recipients and the traits selected for or against are so selected for the sake of their beneficial/costly effect on the evolutionary contribution of those fitness-recipients.

The proof for this definition goes as follows. Let us assume that objects of some kind form a level of selection only if those objects satisfy conditions satisfied by all selection mechanisms. That is, all selection mechanisms have something in common which makes them selection mechanisms. Which of the four roles just defined, all of which are found in most historical selective situations, are found in all selection mechanisms? Certainly Darwin's model captures one selection mechanism. On Darwin's model there are fitness-donors and fitness-recipients, but no fitness-effectors or fitness-effectees. That is exactly why the deer example is problematic -it involves unforeseen causes and effects! Fitness-effectors and fitness-effectees exist in the environment in which Darwinian selection operates, but they are not part of the mechanism itself. So a level of selection cannot consist in fitness-effectors or fitness-effectees. The remaining candidates are fitness-donors and fitness-recipients. (There are models in which fitness-effectors and/or fitness-recipients play a role. But such models do not model a unique selection mechanism as such, just the consequences of a selection mechanism in a context which includes a complex causal network).

No matter how complex or innovative a selection model might be, it must incorporate the conditions which qualify Darwinian individual selection as a selection mechanism. Let us clarify these conditions by abstracting away from Darwin's model his assumption that the same organism counts both as fitness-donor and fitness-recipient. A basic selection mechanism exists if and only if (a) some objects of kind D have variable traits which confer on objects of kind R higher fitnesses than other objects of kind R are given in virtue of the traits of other objects of kind D; (b) these traits are causal factors in the (genetic) representation of objects of kind R in future generations of their evolving population; (c) these traits are selected for or against for the

sake of their beneficial/costly effect on the evolutionary contribution of objects of kind R; (d) there is selection between objects of kind R on the basis of the satisfaction of conditions (a), (b) and (c).

Clause (a) discriminates fitness-donors (objects of kind D) from fitness-recipients (objects of kind R). Clause (b) employs the causal concept 'selection for properties'. Clause (c) employs the functional concept 'selection for the sake of'. Clause (d) employs the vague notion 'selection between objects' so as to hook up with causal and functional concepts in a way that the consequentialist notion 'selection of objects' does not. Given pre-analytic intuition (P), clause (d) unpacks the root ontological notion that there is selection between objects of kind R as objects of kind R.

On Darwin's model, suitably generalized, there is selection between fitness-recipients as such but there is no selection between fitness-donors as such. It follows that objects having the role of fitness-donors do not form levels of selection. It follows that objects having the role of fitness-recipients do form levels of selection. The basic selection mechanism clarifies the functionalist definition (3c) in non-technical terms. *Objects of some biological kind form a level of selection if and only if there is selection between those objects on the basis of their differential fitnesses, which are determined by traits selected for or against for the sake of their effect on the evolutionary contribution of those objects.*

(4c) Any definition of the level should explain not only why traits become prevalent or rare when selection occurs and fitnesses vary, but also why traits selected for or against are so selected. The consequentialist concept 'selection of objects' helps explain the relative frequency of traits. The causal concept 'selection for properties' helps explain why fitnesses vary. The functional concept 'selection for the sake of' helps explain why traits are selected for or against. Traits are positively or negatively selected because of their effect on the evolutionary contribution of the members of the relevant evolving population.

From the perspective of functional analysis, other approaches fail to make the needed discriminations. Consequentialist analysis fails because it cannot discriminate between fitness-recipients and fitness-effectees; in both cases there is selection of objects. It is that fact

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which gives the power to charge that consequentialism cannot make sense of the objective distinctness of levels of selection. Causal analysis fails because it cannot discriminate between fitness-donors and fitness-effectors; in both cases there is selection for traits. It is that fact which gives force to the charge that causalism cannot define the level with requisite generality.

Consequentialist, causal, and functional analyses appeal to successively richer concepts to define the level. Selection of objects does not imply selection for or against the traits of those objects; traits may change in frequency even though those traits do not cause or hinder reproductive success. Selection for or against traits of some object does not imply selection for or against those traits for the sake of their effect on that object's evolutionary contribution; those traits may cause or hinder the reproductive success of another object rather than that very object. It would be a great mistake not to distinguish functions from effects even though functions involve effects. Suppose that the differential fitnesses of some fitness-recipients are correlated with the differential fitnesses of some other objects. It follows that these other objects are fitness-effectees but not that they are fitness-recipients. So selection of objects does not imply selection for the sake of those objects' evolutionary contribution.

This functionalist analysis suggests a natural taxonomy of traditional and recent selection models, revealing all as variants on the same basic selection mechanism. In Darwinian selection, the same individual is both fitness-donor and fitness-recipient. In selection for altruistic benefits to other individuals, non-identical individuals are fitness-donors and fitness-recipients. In selection for altruistic benefits to the individual's group, individuals are fitness-donors and the group is the fitness-recipient. In selection for species traits which enhance their rate of branching and persistence, the same group is both fitness-donor and fitness-recipient. When individual fitnesses are determined by group membership and group traits, groups are fitness effectors and the same individual is both fitness-donor and fitness-recipient. In kin selection, when an individual's interests are promoted by relations to close relatives, there is kinship effect on individual fitness and so related individuals are close relatives but the same individual is both fitness-donor and fitness-recipient. In parental manipulation, when a parent uses an

offspring to favor that parent's interests, there is an offspring effect on parental fitness and so offspring are fitness-effectors but the same individual is both fitness-donor and fitness-recipient. In reciprocal altruism, when an individual's fitness is promoted by favors to others in hope of return, there is an effect of others on individual fitness and so reciprocating individuals are fitness-effectors but the same individual is both fitness-donor and fitness-recipient. It should be clear how to apply these terms to other forms of selection.

Hence, the analysis justifies our tendency to regard models of group membership, kin selection, parental manipulation, and reciprocal altruism as form of individual selection. The analysis also justifies our tendency to regard models of altruism toward groups and certain forms of species selection as group selection. While these generalizations hold, they are not inviolable; one must look at the specifics of each model and decide which objects play which of the four roles on that model in order to decide at what level selection occurs on that model. Even more impressive, the analysis anticipates as yet undevised models which apply similar factors to fitness-effectors and/or fitness-effectees at various levels. Like Mendeleev's Table, the analysis may aid progress by pointing out unforeseen possibilities for us to study observationally and theoretically.

How well does functional analysis fulfill our regulative ideal? It not only offers help in deciding problematic cases, but also does justice to both the intuition that group selection occurs and that it is merely apparent in the fleet deer example. It delivers a definition which is logically precise and general. It points out what is constant and what is variable in various selection regimes, permitting the objective difference among levels of selection. But such illumination is purchased at the price of seeming insecurity. The concepts 'selection for the sake of' and 'evolutionary contribution' confront a dilemma: either the analysis is trivial (e.g. 'selection for the sake of' is not functional and means 'selection in virtue of' and 'evolutionary contribution' is not functional and merely means 'evolutionary consequences') or else the analysis is genuinely functional but then obviously false or unacceptably problematic. To blunt the initial force of this dilemma (I cannot claim to dissolve it, as each mode of analysis has its own anomalies), let us consider it in relation to the levels/units issue.

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The Levels/Units Issue. Brandon's and Burian's anthology (1984) highlights the fact that the state of analytic ontology concerning natural selection now turns on the relation between the levels and units of selection concepts. One group (e.g. Wimsatt, Lewontin, Sober) treats them as equivalent. Another group (e.g. Hull, Dawkins, Brandon) treats them as distinct. I shall argue that this issue turns in the relation between selection and evolution.

Suppose our analysis begins from the following fact: (5b) variable properties provide conditions for selection via effects on reproductive success. Then we will find motivations to distinguish context-dependent from context-independent effects (Wimsatt), univocal from contextually variable causal roles (Lewontin, Sober), or make related causal distinctions. These provide resources against genic selectionism. Such causal distinctions are then used to show that single genes do not usually form levels of selection. Wimsatt argues that epistatic interactions prevent single genes from satisfying the causal conditions of *levels of selection*. Sober argues that polygeny rather than epistasis provides the counterexample. They infer that single genes are not usually units of selection. But that does not follow unless it is assumed that the levels and units concepts are equivalent. Causal analysts are thus committed to reading (6) as: (6b) the levels and units of selection concepts have equivalent causal contents.

But suppose we begin our analysis by focusing on the following fact: (5c) the replication of genes drives evolutionary change in a way not found at other levels. Then we will find motivations to distinguish replicators from interactors (Hull), replicators from vehicles (Dawkins), or make related distinctions. Causal arguments against genic selectionism will never be regarded as refutations, no matter how clever they are. Causal arguments concern the levels problem, not the units problem (Brandon). So we hold that the levels problem concerns what objects count as interactors (Hull) or vehicles (Dawkins) whereas the units problem concerns what objects count as replicators (Dawkins). Each denies that the levels and units concepts are equivalent. But to do so because the differential replication of genes is the most fundamental consequence of selection would be to adopt the consequentialist approach already debunked. So I propose to read (6) as: (6c) the levels and units concepts have distinct functional contents.

Everyone agrees that there can be selection without evolution in the sense than other evolutionary forces may counteract the effects of selection. Everyone agrees that evolution by selection implies heritable differential fitness. Everyone agrees that genes are requires for heritability. But Sober believes that selection can occur without evolution occurring in the sense that the traits selected for may not have a suitable genetic basis. Dawkins must disagree if he is to maintain that the gene is always the unit of selection. He must hold that if a trait is not genetic then not only can there be no evolution by selection for or against that trait, there can be no selection at all. These point show that the debate rests on whether the concept of unit of selection has intrinsic evolutionary content. The Wimsatt-Lewontin-Sober approach treats selection as conceptually basic and evolution as derivative. The Hull-Dawkins approach treats evolution as conceptually basic and selection as derivative. Yet neither side writes as if they recognize that this is the crucial issue which divides them.

The historical origin of this issue can be traced all the way back to Darwin's summary statement of how natural selection works (1859, p. 170):

But if variations useful to any organic being do occur, assuredly individuals thus characterized will have best chance of being preserved in the struggle for life: and from the strong principle of inheritance they will tend to produce offspring similarly characterized. This principle of preservation, I have called, for the sake of brevity, Natural Selection.

Darwin's statement is vague in that his principle encompasses both *selection and evolution by selection*. Is selection by its nature a mode of evolution, i.e., is evolution basic and selection derivative? Or is selection a force which can be conceived independently of evolution, i.e., is selection basic and evolution by selection derivative? Sober (1984, p. 50) conceives selection as limited to Darwin's "useful variations", i.e., the circumstances which produce selective forces considered independently of how those forces produce evolutionary changes. The variable traits involved need not have a specific genetic basis to satisfy Sober's causal description of a level of selection. He thinks that selection implies differential fitness but not heritability. Dawkins evidently

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conceives selection as encompassing both useful variations and a principle of inherence; so he takes selection to imply heritable differential fitness, a presupposition of genic selectionism.

As the Sober-Dawkins debate now stands, Sober has the upper hand over Dawkins in that Sober is but Dawkins is not clear on what sort of concepts his analysis appeals to. Dawkins invokes consequentialist arguments (e.g. the representability of all selection using genic fitnesses by averaging over contexts), causal arguments (genes cause phenotypic traits which in turn cause reproductive success and so genes cause reproductive success), and teleological arguments (organisms, groups and other levels exist in order that the genes within them perpetuate themselves). Although Sober has located many holes in Dawkins' consequentialist and causal arguments, he has not even attempted to deal explicitly with Dawkins' teleological language.

I shall use statements made by E.O. Wilson, Williams, and Dawkins to illustrate their presupposition, namely that the unit is to be conceived via teleological, evolutionary, genetic and cost/benefit concepts. But Sober's definition of group selection explicates the unit (as equivalent to the level) using causal concepts without any reference to anything evolutionary or genetic. So Sober's causal analysis turns on its head the usual way evolutionary biologists view the unit of selection. (See Holcomb 1986-87 for the details and for an overview of the debate as a whole in terms of the contrast between a "unit of possession" (i.e. fitness-donor) and a "unit of benefit" (i.e. fitness-recipient). In that paper Holcomb failed to realize that pre-analytic intuition (P) prevents us from claiming that a level is a pair consisting of both donors and recipients. If we give up (P) and regard the levels and units concepts as equivalent, that claim remains viable).

Consider in this regard Wilson's claim (1975, p. 4) that the blends of aggression and fear we experience are "designed not to promote the happiness and survival of the individual, but to favor the maximum transmission of the controlling genes"... "as a result of the balance of counteracting selection forces at different levels", whereby "what is good for" one level may be "destructive to" other levels. Such language reflects commitments about the unit which differentiates it from the level. It concerns what object a trait "is good for", i.e., a locus of costs/benefits. It concerns the "maximum transmission of controlling

genes", i.e., a genetic unit. It concerns whose interests traits are "designed" by selection to favor, i.e., a teleological unit. It concerns the results of "counteracting selection forces at different levels", i.e., an evolutionary unit.

Williams' (1986) critique of Sober's book maintains that selection acts "at the level of alternative alleles" (p. 115), i.e., the unit is genetic. He holds that organisms "lack continuity (across generations) and cannot be entities preserved or extinguished by natural selection" (p. 116), i.e., the unit is evolutionary. He writes (1966, p. 8) that "natural selection... can only produce adaptations for the genetic survival of individuals", i.e., the unit is teleological, genetic and the locus of cost/benefits.

Dawkins (1982a, p. 45) begins "If we wish to speak teleologically, all adaptations are for the preservation of DNA; DNA just is", i.e., the unit is teleological. He (1982, p. 81) defines the unit as the "optimon", namely "the entity for whose benefit adaptations may be said to exist", i.e., the unit is teleological and the locus of costs/benefits. He argues that the optimon is an active germ-line replicator, i.e., the unit is genetic and evolutionary.

Perhaps Sober ignores such language because he regards teleological talk about selection and evolution as merely heuristic and as literally false. Faber (1986) is not the first to argue persuasively against understanding natural selection in teleological terms. He holds (pp. 114-116) that a selection process is teleological, not mere sorting, only if it involves at least two distinct things, a selector and a selectee (which is not the case in natural selection) and only if the selector performs its sorting with an orientation toward some goal or future state (which is not the case in natural selection). Selection is not a teleological process.

However, such teleological talk has a use which should not be lightly dismissed. It serves to justify our taking the gene to be the unit of selection and our tendency to differentiate the unit from the level. I think that if we are to justify these two related proposals at all, we need a functional analysis which is *prima facie* richer than a consequentialist or causal analysis but not a full blown teleological analysis. The following extension of the previous functional analysis is designed to meet this condition, with the caveat that further explica-

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tion may show it to be reducible to a species of causal or teleological analysis. For instance, it is consistent with my thesis that the same facts establish either causality or function, depending upon where your focus of attention is at the moment; if so a functional analysis is as legitimate as a causal analysis.

The functional analysis of the level of selection used two *prima facie* functional concepts, namely 'selection for the sake of' and 'evolutionary contribution'. 'Selection for the sake of' is not the teleological 'selection in order that'; traits are not selected for or against in order that genes, organisms, or groups benefit or suffer. 'Selection for the sake of' merely implies 'selection on the basis of a criterion'. True, there is nothing intrinsically causal or functional about the latter concept. Even so, 'selection for the sake of' gains causal content because the criterion itself is specified causally, i.e., a trait is selected for if it increases the chances of (probabilistically causes) reproductive success. And 'selection for the sake of' gains functional content because the criterion so specified is correctly specified on functional grounds, i.e., in terms of the relative contribution of parts (members of an evolving population) to a whole (that population). Hence, the unit concept has both causal and functional content.

To "*contribute*" is to play a significant part in bringing about some result or end. Assuming the neo-Darwinian view of evolution (Le-wontin, in Sober 1984a, p. 9), "*evolution*" is the conversion of variation between members of a population into variation between successive generations of that population. "*Evolution by selection*" in its strict sense is evolution in which the variation between population members so converted is variation between fitness-recipients. A "*fitness-transmitter*" is whatever physical object exists by means of which variations among fitness-recipients enable them to differentially contribute to the ancestry of future generations. A "*fitness-locus*" is that evolving population to which a fitness-transmitter transmits such differential contributions. Although fitness differences are properly identified in a proximate sense by reference to fitness-recipients (levels of selection), they are properly identified in the ultimate sense by reference to evolving populations.

These technical terms capture a way of thought prevalent in evolutionary biology ever since Fisher. For instance,

At the organismic level, Fisher (1930) identified fitness with the Malthusian parameter (intrinsic rate of increase), since this parameter reflects representation in future generations and provides an objective basis for the comparison of evolutionary success between individuals. (Arnold and Fristrup, in Brandon and Burian, 1984).

In devising the formula for reproductive value, Fisher (1958, p. 27) asks

To what extent will persons of this (a given) age, on the average, contribute to the ancestry of future generations? The question is one of some interest since the direct action of Natural Selection must be proportional to this contribution.

Fitness, by definition, is the measure of the extent to which population members exhibiting some variable trait, on the average, contribute to the ancestry of future generations. "Direct contributions" are those which proceed from a given member's personal survival and reproduction. "Indirect contributions" are those which proceed from a given member's effects on the survival and reproduction of others. "Inclusive fitness" is a joint measure of an individual's (genetic) representation in descendant generations. But no contribution, no matter how direct or indirect, will occur unless it is transmitted in some form across generations. That is why we need to think of fitness-transmitters in conceiving of selection occurring at all. Thus we are driven to define a "unit of selection" as a "fitness-transmitter".

It follows from these definitions that the levels and units of selection concepts have distinct functional contents. *A level of selection is a fitness-recipient, whereas a unit of selection is a fitness-transmitter.* The levels problem concerns which objects count as fitness-recipients. the units problem concerns which objects count as fitness-transmitters.

Genes, like organisms and groups, have variable traits which enable them to play the role of fitness-recipients. Genes, unlike organisms and groups, are passed on in the form of physical copies from one generation to another. So genes count as fitness-transmitters, whereas organisms and groups do not. This analysis distinguishes the level from the unit in the tradition of Fisher, Williams, E.O. Wilson, Dawkins, and Hull, but without teleological lingo. Organisms and groups do not

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exist in order that genes perpetuate themselves. Nor is the transmission of genes a goal, purpose or end of organisms or groups. The locus of the evolutionary contribution of a trait selected for or against is the evolving population to which population members acting as relevant fitness-recipients contribute. Genes are merely items whose existence is necessary for a trait to make a difference to the evolutionary contributions of population members. Geneticists sometimes define selection as "the differential reproduction of alternative genetic variants" or as "the differential survival of genes" because those processes enable evolutionary contributions to occur.

Causal analysts and functional analysts understand the theory of evolution by selection by focusing on opposite ends of a single chain of events. Causal analysts start their analysis by focusing on population members and their traits. Next they relate traits to survival and reproductive success (a causal relation). Then they relate survival and reproductive success to evolutionary change (another causal relation). Heritability is required for the latter relation but not for the former to actually obtain. Hence, causal analysts claim that selection does not imply heritability. Functional analysts start their analysis by focusing on evolving populations and their qualities. Then they relate population properties to the contributions by members in previous generations (a functional relation). Unlike functions which are analyzable in terms of the achievement of goal-states or other goods, evolutionary contributions made by members are constitutive of the evolving population. Which objects reproduce and which do not determine the make-up of the evolving population, i.e., its very being rather than its welfare. Then functional analysts relate those members' contributions to the traits of the members themselves (another functional relation). Heritability is required for the former relation to obtain, and derivatively, for the second as well. Hence, functional analysts claim that selection does indeed imply heritability; a trait selected for or against would not be so selected unless it were transmissible in some form.

Which approach is superior? I have tried to show that each approach contains a tightly integrated set of claims of various types, namely claims taking a stand on (1)-(6). One cannot offer criticisms of arguments concerning how best to define the level or unit without also becoming embroiled in debate over pre-analytic intuitions about

problematic cases, the relative roles of various conceptual resources, what does and what does not need explaining, the relation between the levels and the units of selection, the relation between fitness and selection and evolution, and how to satisfy regulative ideals for giving a conceptual analysis. No single argument will be decisive in the absence of considering a series of interlocking arguments from each side concerning all these types of claims. Other issues being equal, the following argument does tip the scales in favor of the functional approach: causal analysts are committed to conceiving selection as logically independent of evolution, which prevents them from accounting for why fitness is correctly identified with survival and reproductive success.

Sober simply assumes that the effects which make for fitness-differences are measured using fitness so identified. But if we ignore the contributory relation between populations and their members, there is no logical reason why fitness should not be identified with something else. Why shouldn't we identify fitness with adaptiveness in the sense of physiological health at the organismic level or with adaptiveness in the sense of diversity at the species level? Why not count success in terms of survival alone, with no reference to reproduction? To say that the better adapted tend to leave more offspring is merely to cite a possible effect of adaptiveness. On a causal analysis, possible effects do not count for much. If transmission of genes is a possible effect to be discounted as irrelevant when conceiving the unit, then by parity of reasoning so should leaving more offspring!

Ayala and Valentine (1979, p. 11) express the consensus view which suggests the superiority of functional over causal analysis:

As Darwin saw it, natural selection may be due to either differential survival or to differential fertility or to both. Differential rate of development, differential mating success, and differences in other components of the life cycle may contribute to natural selection, but these may be subsumed under survival and fertility. In fact, all components of the process of natural selection may be simply incorporated under differential reproduction; differential survival, mating success, and so on, result in natural selection only if they become translated into differential reproduction.

The underlying rationale here must be that differential reproduction

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is the only way organisms contribute to the ancestry of future generations. Thus the functional approach explains what the causal approach can only assume, namely why fitness is correctly identified the way it is. Given that the ground for identifying fitness correctly goes to the conceptual heart of selection theory, the greater explanatory power of the functional approach makes it far superior to the causal approach.

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